

Light availability indirectly limits herbivore growth and abundance in a high rocky intertidal community during the winter

Abstract—Light availability and consumer pressure are fundamental factors that structure aquatic communities, but their integrated effects are rarely studied in marine benthic systems. Using a factorial experiment, I investigated the effects of light availability and grazing by limpets (*Lottia digitalis*) to determine the relative influence of each on the growth and abundance of producers and consumers in a rocky intertidal community during the winter. Light reduction via shading reduced the abundance of filamentous algae and reduced the abundance of the herbivorous periwinkle *Littorina sitkana*. The effects of limpet grazing reduced the abundance of filamentous algae, *Porphyra* spp., and diatom mats. Higher limpet densities were also associated with significantly lower densities of adult, but not juvenile, *Littorina* spp. Light and limpet density interacted to determine *Lottia* growth, which was high in unshaded, single-limpet enclosures but was negligible in plots with two limpets, shades, or both. Variation in bottom-up (resource-driven) and top-down (consumer-driven) forces are important determinants of abundance at both trophic levels, but the effects are complex, taxon-specific, and, for littorine snails, size-specific. Because the study species accomplish most of their growth and reproduction during the winter, the interplay of light and herbivory during this season will likely influence long-term community dynamics.

Recent ecological synthesis has provided substantial evidence that top-down and bottom-up processes act in concert to structure biological communities (Menge 2000). The general acceptance of this view over the past decade has motivated a growing number of studies that have simultaneously manipulated top-down and bottom-up factors. In marine benthic systems, these studies have generally taken the form of factorial manipulations of consumer abundance and nutrient supply (Neckles et al. 1993; Wootton et al. 1996; Hillebrand et al. 2000; Lotze et al. 2001). Although nutrient supply is clearly important, very little attention has been devoted to spatial and temporal variability in another fundamental bottom-up factor: light. Light is the ultimate bottom-up force, powering the vast majority of global primary production. In marine systems, light varies locally with depth, turbidity, and substrate orientation; regionally with patterns of cloud cover; globally with latitude; and temporally with the seasons. Light limitation has been documented in a variety of marine systems (e.g., kelp forests, Reed and Foster 1984; benthic microalgal assemblages, Blanchard and Montagna 1992; seagrass beds, Ruiz and Romero 2001; and coral reefs, Stimson 1985 and references therein). Because patterns of irradiance and nutrient concentration are largely independent, variation in light availability has the potential to interact with top-down variables in unique ways to control spatial and temporal patterns of species distribution and abundance at a variety of scales. In this study, I examined the effects of light

and the effects of a dominant molluscan herbivore on a rocky intertidal community.

This research was conducted during the winter of 1998–1999 on Tatoosh Island (48°23.5'N, 124°44.2'W), located just off the coast of Washington State. Winter air temperatures on Tatoosh are consistently cool but rarely drop below freezing. Light availability to intertidal autotrophs in winter is restricted by tidal patterns (the majority of the intertidal zone is submerged during daylight hours), heavy wave action, overcast skies, short days, and a low incident angle of direct solar radiation. The experimental area used in this study was just above the *Balanus glandula* zone (~2.3 m above mean lower low water) on a south-facing vertical cliff. In the study area, microalgae are the dominant primary producers, along with winter blooms of various foliose algae (e.g., *Porphyra*, *Urospora*, *Bangia*, and *Enteromorpha*). Sessile invertebrates (e.g., barnacles) were rare. The dominant grazer, by total biomass, is the acmaeid limpet *Lottia digitalis*. Other numerically abundant grazers include the periwinkles *Littorina sitkana*, *Littorina plena*, and *Littorina subrotundata* (sensu Reid 1996). As a result of the steep slope angle, high intertidal position, and high wave energy, macro-predators (birds, crabs, and carnivorous gastropods) were never seen foraging at this location.

I used a factorial design to investigate the effects of winter light availability and limpet grazing on the abundance of algae, the growth of limpets, and the abundance of other herbivores. The experiment was restricted to the winter season for the following reasons. First, light is most likely to be limiting during the winter—Tatoosh receives ~15% as much light per day in December as it does in June (Helmuth and Harley unpubl. data). Second, shade artifacts (e.g., reduced temperature and desiccation) become problematic during the summer (see below). Finally, the species under investigation generally accomplish most, if not all, of their growth and reproduction during the winter (Frank 1965; Nicotri 1977; Cubit 1984; Shanks 1988).

Experimental plots consisted of a copper ring (2.5 cm tall × 15 cm diameter) attached to the rock with Sea Goin' Poxy Putty (Permalite Plastics, Inc.). Limpets rarely cross metallic copper barriers (Johnson 1992), although copper rings do not restrict the emigration or immigration of littorine snails over the long term (author's pers. observation). The rock surface inside the rings was not scraped or otherwise manipulated. Nevertheless, no micro- or macroalgae were visibly evident within the plots at the beginning of the experiment (8 October 1998). Each plot was haphazardly assigned to one of two irradiance treatments (shaded or unshaded), which were well interspersed. Within shade treatments, limpet treatments (zero, one, or two *L. digitalis*) were assigned randomly, and each treatment combination was replicated six times. All plots ($n = 36$) were located in a single row at the same tidal

height and were separated by <5 cm except in a few positions where the row was interrupted by large (>5 cm diameter) granitic inclusions in the otherwise small-grained rock matrix.

Medium-sized (11–14 mm) *L. digitalis* were collected from nearby areas and marked with red Testor's modeling paint. Limpet lengths were measured to the nearest tenth of a millimeter with calipers. The experimental limpets were, on average, 8–10 mm smaller than the largest naturally occurring limpets, which allowed a greater scope for growth. Natural limpet densities (mean \pm standard error, 0.75 ± 0.15 100 cm^{-2} as based on 36 randomly placed 100 cm^2 quadrants) fell between the densities in one and two limpet enclosures (0.57 and 1.13 limpets 100 cm^{-2} , respectively).

Because light addition treatments are impractical in intertidal environments, I chose to reduce light via experimental shades on a brightly lit south-facing surface. Shades consisted of heavy duty vexas shade cloth attached to a frame of vinyl-coated shrimp trap material with a mesh size of 1.25×2.5 cm. The shades were attached to the rock via stainless steel screw eyes anchored in quarter-inch nylon wall anchors. This arrangement left ~ 6 cm of open space between the shades and the rock surface. Relative light reduction under the shades was measured with a Sekonic Digilite incident light meter (model L-328, Sekonic Co., Ltd.) and converted to $\mu\text{mol m}^{-2} \text{ s}^{-1}$ according to the method of Thimijan and Heins (1983). On a sunny day in January, shades reduced light levels from 1,180 to 480 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ at 1230 h and from 590 to 200 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ at 1530 h. On an overcast day in February, shades reduced light levels from 110 to 46 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. Thus, shades reduced incident light by $\sim 60\%$ – 65% under a variety of conditions. By comparison, a north-facing wall receives 90% less light than a south facing wall on a sunny day and 55% less light on an overcast day. Because of the low angle of the sun on Tatoosh Island during the winter, even horizontal surfaces receive less direct sunlight than south-facing walls from October through March. Shades on a south-facing wall therefore mimic irradiance conditions in other areas in the intertidal.

Experimental shades have the potential to influence water flow and thermal and desiccation stress in addition to light intensity. Shade controls were not used because even the wire mesh without vexas casts a substantial amount of shade, and shade control data would therefore be difficult to interpret (see also Johnson 1992). However, I believe that unintended shade artifacts were minimal for the following reasons. In terms of wave shock and water flow, waves surged parallel to the wall at the experimental site rather than breaking against it. Because the shades were open in the along-shore directions, hydrodynamic influences should have been minimized. To test this assumption, I deployed dissolution blocks, which dissolve at a rate proportional to water flux (Wildish and Kristmanson 1997), for 3 d (five high tides). Dissolution blocks ($n = 12$) consisted of Lightweight Hydrocal (Woodland Scenics, Inc.) that had set around a screw in film canister molds. Rates of dissolution per tide were similar between shaded and nonshaded treatments; the shaded dissolution block mass loss (mean \pm standard error) was $10.9 \pm 0.3\%$ per tide, whereas unshaded dissolution blocks lost $10.3 \pm 0.3\%$ of their mass per tide. This difference was

not significant (one-way analysis of variance [ANOVA] performed on arcsine square root-transformed data: $F_{1,10} = 2.19$, $P = 0.17$). Furthermore, although shades reduce the maximum temperature difference between emersed and immersed conditions by $\sim 25\%$ on long summer days (Harley and Lopez unpubl. data), any such differences were likely negligible during the winter, when days were short and solar heating was minimal. Average daily maximum temperatures recorded in the high intertidal from 26 October to 27 March 2001 were 11.9 ± 3.36 $^{\circ}\text{C}$ (mean \pm standard deviation), $\sim 2^{\circ}\text{C}$ above sea water temperature, on average (Helmuth and Harley unpubl. data). Summer substrate temperatures, by comparison, regularly were $>35^{\circ}\text{C}$ (Harley and Helmuth unpubl. data). Finally, shades may have reduced desiccation stress, even though desiccation stress is also minimal during the winter (Underwood and Jernakoff 1984). However, reduced desiccation stress would favor both herbivores and algae (Knox 2001 and references therein) and would thus work in the opposite direction of the hypothesized light effects. In this sense, the experimental shades are a conservative estimate of the total impact of light.

Experimental plots were censused and photographed on 27 March 1999. At this time, 34 of the initial 36 limpets remained in their original rings. Limpets were lost from a shaded two-limpet plot and an unshaded one-limpet plot. Because the exact date of loss was unknown, these two plots were discarded from the analyses. At least one of these limpets escaped, rather than died, because a marked limpet was found outside the enclosures. Within the plots, littorine snails were counted and identified to species. Snails <2 mm were difficult to identify reliably and were categorized as "juvenile *Littorina*." Individual *Porphyra* sp. thalli were counted, and diatom mats were noted as present or absent. A mixture of macroscopic algae, composed primarily of *Bangia*, *Urosopora*, and *Enteromorpha*, grew on the rock and epoxy putty surfaces inside some rings (macroscopic algae were never observed on putty or nearby rock surfaces outside the rings). The cover of these species (hereafter "filamentous algae") was estimated from photographs by measuring the number of degrees of the epoxy circle that were covered with the algae. Accurate photograph-based cover estimates on the darker rock background were prohibitively difficult; however, the algal cover on the epoxy was representative of the algal cover on the adjacent rock (author's pers. observation). Photographs were analyzed without observer knowledge of the treatment combination, to prevent bias in cover estimation. Although I was unable to quantify micro- or macroalgal biomass in the field, my methods provide accurate estimates of relative algal abundance, which are sufficient to identify patterns with respect to shading and herbivory.

Limpets were not remeasured until 18 April 1999. Unfortunately, two additional limpets had escaped by this time: one from an unshaded one-limpet plot and one from a shaded two-limpet plot. All remaining limpets ($n = 32$) were remeasured with calipers, and growth was obtained by subtracting the initial length from the final length.

Statistical analyses were performed by use of JMP version 3.2.6 (SAS Institute). The lack of variance for filamentous algal cover and *Porphyra* abundance in certain treatments necessitated the use of a two-factor Kruskal-Wallis test (Zar

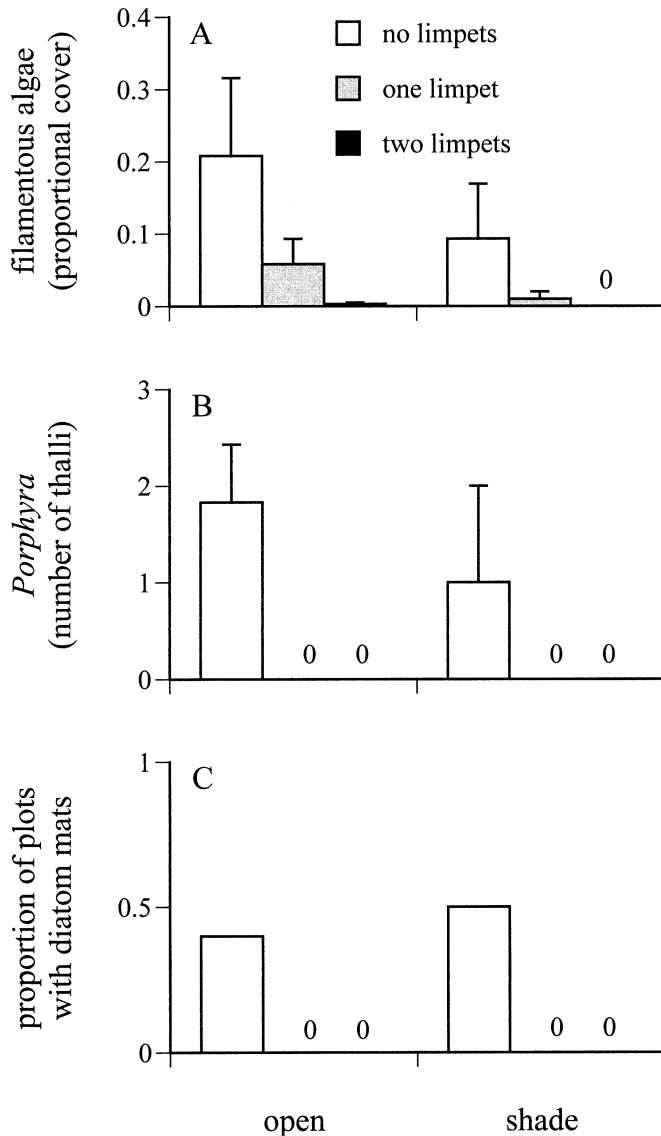


Fig. 1. Effects of light and limpet abundance on algae. (A) Proportion of interior epoxy covered by filamentous algae. (B) Abundance of *Porphyra* thalli. (C) Relative abundance of diatom mats. Data are means of five replicates for the open, one-limpet treatment and the shaded, two-limpet treatment and six replicates for the remaining treatments. Error bars are standard errors.

1984). For this test, missing data ($n = 2$) were estimated according to the method of Shearer (1973). For two-way ANOVA (shade and limpet treatments), limpet density was considered ordinal. Limpet growth for the two-limpet treatments was averaged for each plot to avoid pseudoreplication. Although the assumption of equal variance was met in all cases, juvenile *Littorina* spp. abundance data were not normally distributed. This bias was not correctable through transformations of the data. For consistency, these data were analyzed in the same (parametric) manner as the other littorine data; however, the results for juveniles should be interpreted with caution.

At the end of the experiment, filamentous algae, *Porphyra*, and diatom mats were present in the experimental plots.

Table 1. Results of two-factor (shade and limpet density) Kruskal-Wallis tests for filamentous algae and *Porphyra*. Significant effects ($\alpha = 0.05$) are shown in boldface type.

Effect	H	P
Filamentous algae		
Shade	5.87	<0.025
Limpet	9.81	<0.01
Shade \times limpet	0.62	>0.5
<i>Porphyra</i>		
Shade	0.94	>0.25
Limpet	6.08	<0.05
Shade \times limpet	1.88	>0.25

Filamentous algae were more abundant in unshaded treatments and in areas from which limpets had been removed (Fig. 1A). The shade and limpet effects were both significant, and there was no interaction between main effects (Table 1). *Porphyra*, although common on Tatoosh in the winter, was rare in the study plots. It occurred only in areas with no limpets (Fig. 1B), where it was significantly more abundant than in treatments with limpets (Table 1). *Porphyra* abundance did not differ between unshaded and shaded areas, and there was no shade \times limpet interaction (Table 1). As with *Porphyra*, diatom mats were only found in areas where limpets could not forage (Fig. 1C). Because of the small number of plots with visible diatom cover, the one- and two-limpet treatments were collapsed for statistical analysis. A single-effect chi-square test confirmed that diatom mats were more abundant in limpet enclosures than limpet enclosures (likelihood ratio, $\chi^2 = 12.1$, $P < 0.001$). Diatom mats were not influenced by shade treatment (likelihood ratio, $\chi^2 = 0.24$, $P > 0.5$).

Limpet growth was not related to initial limpet length (regression with treatment as a blocking factor, $P = 0.42$), so initial size was not used as a covariate in the growth analysis. Limpets grew well when enclosed alone in unshaded plots but not in plots under shades, with a second limpet, or both (Fig. 2). Of the four treatment combinations, only the growth in unshaded, uncrowded plots differed significantly from zero (t test, $n = 4$, $P = 0.041$). In the two-factor ANOVA, the shade \times limpet interaction term was significant, which indicates that the effect of intraspecific competition on growth depended on the light environment (Table 2). In unshaded treatments, a reduction of limpet density from two per plot to one per plot resulted in greatly increased limpet growth. In shaded treatments, algal resources were evidently too scarce to support the growth of even a single limpet, and

Table 2. Results of two-factor (shade and limpet density) ANOVA on limpet growth. Significant effects ($\alpha = 0.05$) are shown in boldface type.

Effect	df	F	P
Shade	1	4.89	0.041
Limpet	1	2.55	0.129
Shade \times limpet	1	5.59	0.030
Error	17		

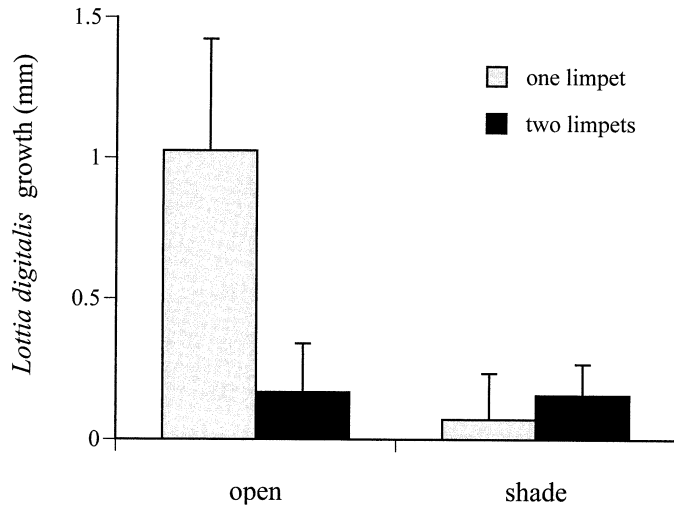


Fig. 2. Effects of light and limpet density on limpet growth over a 192-d period from October through April. Sample sizes are open, one limpet ($n = 4$); open, two limpets ($n = 6$); shaded, one limpet ($n = 6$); and shaded, two limpets ($n = 5$). Error bars are standard errors.

a comparison of single versus double limpet enclosures revealed no differences in limpet growth.

Three species of *Littorina* were present in the experimental plots, although identification to species could only be made for snails >2 mm. Abundance patterns for *L. sitkana*, the numerically dominant herbivore in the experimental arenas, paralleled patterns of algal abundance in the different treatments (Fig. 3A). *L. sitkana* was significantly more abun-

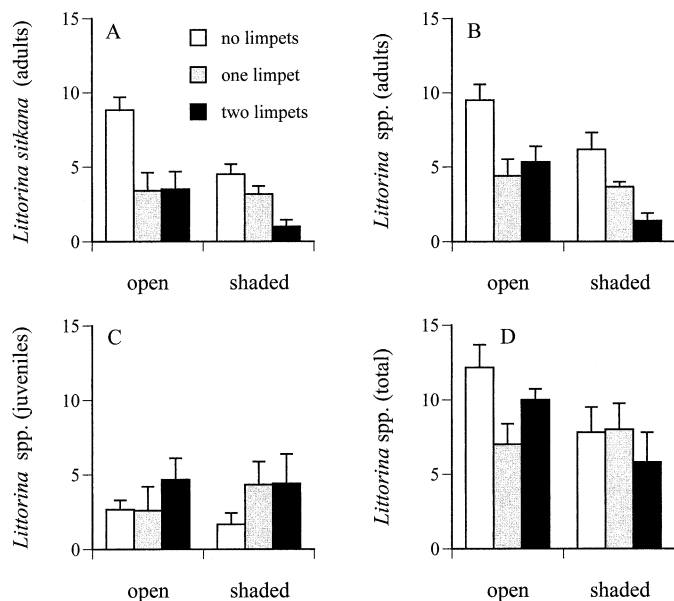


Fig. 3. Effects of light and limpet density on the number of herbivorous snails per experimental plot. (A) Adult *L. sitkana*. (B) Adult *L. sitkana*, *L. subrotundata*, and *L. plena* combined. (C) Juvenile *L. sitkana*, *L. subrotundata*, and *L. plena* combined. (D) All littorine snails combined. Sample sizes are as per Fig. 1, and error bars are standard errors.

Table 3. Results of two-factor (shade and limpet density) ANOVA on the abundance of *Littorina sitkana*, total adult *Littorina* spp., total juvenile *Littorina* spp., and total *Littorina* spp. Alpha values were adjusted by use of a sequential Bonferroni correction (*L. sitkana*; $\alpha = 0.013$; all adults; $\alpha = 0.017$; all *Littorina*; $\alpha = 0.025$; all juveniles; $\alpha = 0.050$). Significant effects are highlighted in boldface type.

Effect	df	F	P
<i>Littorina sitkana</i>			
Shade	1	13.6	0.001
Limpet	2	14.9	<<0.001
Shade \times limpet	2	2.90	0.071
Error	28		
All adult <i>Littorina</i>			
Shade	1	6.70	0.015
Limpet	2	13.5	<<0.001
Shade \times limpet	2	1.60	0.221
Error	28		
All juvenile <i>Littorina</i> *			
Shade	1	0.31	0.585
Limpet	2	3.13	0.060
Shade \times limpet	2	0.69	0.512
Error	28		
All <i>Littorina</i>			
Shade	1	4.19	0.050
Limpet	2	1.33	0.282
Shade \times limpet	2	1.53	0.233
Error	28		

* Note that juvenile *Littorina* abundances were not normally distributed and that the statistical results for juveniles should therefore be interpreted with caution.

dant in unshaded areas and was significantly less abundant in areas with increasing numbers of limpets (Table 3). There was no significant interaction between main effects. *L. plena* and *L. subrotundata* were relatively uncommon (5.1% and 14.7% of total adult littorines, respectively). Neither *L. plena* nor *L. subrotundata* abundance differed significantly among treatments, although the power to detect such differences was low (data not shown). When adult littorines are treated as a group, patterns with regard to light and limpet density treatments were similar to those observed for *L. sitkana* alone (Fig. 3B). The effects of shade and limpet density were both significant (Table 3), with adult littorines being more abundant in treatments with fewer limpets and greater illumination. There was no significant interaction between main effects (Table 3).

Juvenile littorines (<2 mm) represented 41% of the total population of *Littorina* spp. in the experimental plots. In contrast to congeneric adults, juvenile snails exhibited no significant response to shading or limpet density (Table 3). In fact, there was a weak trend toward higher juvenile abundance in plots with more limpets (Fig. 3C). As a result of the qualitatively, if not quantitatively, different responses of adult and juvenile littorines to limpet density effects, the biological patterns found within each size class became obscured when all snails were lumped (Fig. 3D). There was no statistically significant effect of shade, limpet density, or the

shade \times limpet density interaction on the overall abundance of littorines (Table 3).

Light has been shown to limit benthic primary production in a variety of aquatic ecosystems, including lakes (Hawes and Smith 1994), streams and rivers (Rosemond 1993; Hill et al. 1995; Rosemond et al. 2000), estuaries (Blanchard and Montagna 1992), and marine subtidal systems (Ruiz and Romero 2001). By altering primary production, the effects of light can be transmitted to other trophic levels, including herbivores (Hill et al. 1995), predators (Hopkins 1976), and decomposers (Boetius et al. 1996). Despite its obvious importance, light has been largely ignored as a structuring agent in marine intertidal systems. On rocky shores, increasing irradiance is generally accompanied by increasing thermal and desiccation stress, which may be harmful or lethal to intertidal plants and animals (Knox 2001). Therefore, correlations between irradiance and production or abundance tend to be negative, particularly in high shore habitats. High shore algae are generally more productive and/or more abundant in shaded crevices (Anderson and Foster 1999), on north-facing slopes (Castenholz 1963), and during the winter months (Nicotri 1977; Cubit 1984; Underwood 1984). Many high shore herbivores actively seek shaded areas (Little 1989) and accomplish most, if not all, of their growth and reproduction during the winter (Frank 1965; Quinn 1988). Nevertheless, light can be limiting in intertidal systems, especially when the effects of thermal and desiccation stress are minimal. For example, diatoms, in the absence of herbivores, are least abundant on north-facing intertidal surfaces in Oregon during the winter, a result attributed to light limitation (Castenholz 1963). Experimental shading of low intertidal surfaces on a tropical shore, again in the absence of herbivores, resulted in reduced abundances of microalgae and green algal turfs (Williams 1994). In the present study, shading led to significantly reduced cover of filamentous algae. Shading also reduced the growth of *L. digitalis* and the abundance of *L. sitkana*. To my knowledge, this is the first demonstration of light limitation of heterotrophic production in an intertidal system.

In high intertidal communities, light is only likely to be limiting in the winter. Nevertheless, seasonal light limitation may have long-term consequences, depending on the natural history of the taxa in question. The majority of algae in the uppermost intertidal are seasonally abundant in the winter in the northeast Pacific (e.g., Nicotri 1977; Cubit 1984), when light may be limiting (Castenholz 1963; this study). In contrast, high intertidal algal production during the summer is severely limited by thermal and desiccation stress (Cubit 1984). The effects of herbivory are also most pronounced during the summer months, when consumption, even if absolutely lower than in winter, is higher relative to algal production (Cubit 1984). Given the short life cycle of most high shore algae and this array of harsh summer conditions, it is unclear whether the magnitude of the winter bloom in one year influences the magnitude of the bloom during the next. High intertidal herbivores, on the other hand, may live for a number of years. Large *L. sitkana* elsewhere in Washington are at least several years old (Behrens Yamada 1989), and *L. digitalis* in Oregon can live for >6 yr (Frank 1965). Many high intertidal grazers, including *L. digitalis*, essentially

“scrape by” during the summer and undergo bouts of growth and reproduction in winter, when physical conditions moderate and food resources increase (Frank 1965; Shanks 1998). For these species, winter conditions, including light availability, may play a disproportionate role in the lifetime growth and fitness of individuals as well as in long-term population and community dynamics.

Limpets are important in structuring intertidal communities (Knox 2001 and references therein). In this study, *L. digitalis* significantly reduced all three types of algae that I examined, which indicates a strong top-down role for *L. digitalis* in this system. Doubling the density of limpets in unshaded treatments reduced limpet growth to near zero. Intraspecific competition in *L. digitalis* is well documented (Frank 1965). *L. sitkana* was significantly less abundant in enclosures with limpets, which suggests that the two species compete for food. *Lottia* spp. and adult littorines are known to have similar diets (Nicotri 1977). This result, combined with the observation that *L. sitkana* is more abundant in relatively productive unshaded treatments, is consistent with winter food limitation for *L. sitkana*.

The response of juvenile *Littorina* to limpet density, on the other hand, was unexpected. Juvenile littorines were actually more abundant in limpet enclosures, although this trend was not statistically significant. Although the diet of juvenile *Littorina* is unknown, it likely does not contain many of the larger food items consumed by limpets and older conspecifics. Limpets may enhance juvenile littorine's food resources by removing larger algae that are unavailable to juvenile snails; similar positive associations have been noted for other molluscan herbivores (Paine 1980; Dethier and Duggins 1988). Although the exact nature of the association between limpets and juvenile snails remains unclear, the differing responses of the two size classes of *Littorina* illustrates the dangers of treating different ontogenetic stages as ecological equivalents. When all littorines were lumped for analysis, there was no significant effect of limpet treatment or shade, which obscures important interactions among adult snails, limpets, algae, and light.

Work elsewhere has demonstrated the importance of both nutrients and consumers in benthic marine ecosystems (Nekles et al. 1993; Wootton et al. 1996; Hillebrand et al. 2000; Menge 2000; Lotze et al. 2001). The results presented herein show that light can also interact with consumer pressure to alter the growth and abundance of primary and secondary producers. The next logical step is to determine when the various top-down and bottom-up forces (light, nutrients, and consumer pressure) are important and how they interact to structure communities (e.g., Rosemond et al. 2000). Because all three vary independently through space and time and because the relative effects of each will be taxon-specific, this proliferation of variables greatly complicates both ecological interactions and scientific interpretation. Although potentially difficult to achieve, an appreciation of how multiple bottom-up and top-down forces act in concert is essential if we are to understand and predict community and ecosystem variability through space and time.

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